

NOTES ON BARBULA AND PSEUDOCROSSIDIUM (BRYOPSIDA)  
IN NORTH AMERICA AND AN ANNOTATED KEY TO THE TAXA

Richard H. Zander

Clinton Herbarium, Buffalo Museum of Science, Buffalo NY 14211

This preliminary study of Barbula s. lato was prepared in the course of work on taxa of Pottiaceae for the proposed moss floras of Mexico (ed. A.J. Sharp) and of Arctic North America (ed. W.C. Steere, G.S. Mogensen & R.R. Ireland). It is a synthetic treatment based on representative specimens from a wide geographic area and is offered as an alternative to the usual floristic evaluation of species based only on regional collections. In adopting a broader species concept in this and in recent work (Zander, 1977, 1978a, 1978b), I feel that the taxa recognized have gained in biological meaningfulness. Nomenclatural designations for some extreme expressions, permutations of character states, and geographic variants have been lost. But these morphs, in any case, cannot be dealt with by type methodology and the principle of priority, because of lack of clear discontinuities, and must be designated, if at all, by informal names. Gained, hopefully, is a sense of proportion in the recognition of patterns of variation, within and between taxa, that are often interpretable as evolutionary trends or adaptations; the realization that many genera and species of Pottiaceae are widely distributed in the world in geographic patterns often correlating with certain climates or topographic features; and, the practical value of being able to use good technical characters to fairly easily name distinguishable entities in a moss family whose taxonomy has long been reputed to be "cursed" and "difficult and nasty" (Anon., pers. comm.). It is often said that overly broad species concepts are more difficult to correct, at a later time, than overly narrow concepts. However, this is a simplistic view in that most of the effort of present-day revisionary work is in making sense of the overly analytical results of past one-character or regional taxonomy. Such difficulties are discussed at length by Best (1905) who invoked a kind of botanical Manichaeism in early rebellion against atomistic taxonomic attitudes similar to those espoused by Grout (1938a).

"Andro-" and "gynogametophyte" are terms used here instead of "male" and "female plant" because the former terms ought to be used to distinguish sexually differentiated gametophytes (dioicy) while the latter terms refer to sexual differentiation of sporophytes (dioecy). Sporophytes of mosses are always sexless, but the gametophytes may be dioicous or monoicous. Sporophytes of seed-bearing plants may be monoecious or dioecious, but the gametophytes are always dioicous. Dioicy and monoicy are associated with homosporous and the production of gynandrogametophytes, or of both andro- and gynogametophytes, from the same sporangium, but dioecy and monoecy are associated with heterosporous and the production of andro- and

gynogametophytes from different sporangia. Although I consider the substitution of the terms "phyllidium" and "caulidium" for the moss "leaf" and "stem," respectively, to be an unnecessary nicety that does not reflect major genetic differences, the above sexual distinctions are of evolutionary importance and should not be confused or minimized by false homology.

In a study of the very closely related genus Didymodon (Zander, 1978a), I supported the use of Saito's (1975) distinctions between Didymodon and Barbula, which are based largely on gametophyte characters. These were presented in a table. The North American representation of species previously recognized in Barbula are here placed in two genera and included in the same key to facilitate identification.

KEY TO PSEUDOCROSSIDIUM AND SUBGENERA AND SECTIONS OF  
BARBULA IN NORTH AMERICA

1. Upper leaf margins broadly revolute to spiral-revolute, with cells often more strongly chlorophyllose than medial leaf cells; abaxial stereid band of costa usually strong but adaxial band weak or commonly absent; costa usually excurrent as a stout mucro or short awn..... Pseudocrossidium Williams
1. Upper leaf margins narrowly recurved to plane, with cell chlorophyll content equal to that of medial cells; both stereid bands usually clearly differentiated, the adaxial usually present though occasionally weak or absent; costa ending below leaf apex, percurrent or excurrent as a mucro..... 2.
  2. Leaves spatulate, costa excurrent as a sharp mucro, laminal cells smooth, adaxially bulging and abaxially nearly plane, annulus revoluble.....  
..... Barbula subg. Hyophiladelphus (C. Müll.) Zander
  2. Leaves lanceolate to ligulate or ovate, costa subpercurrent to excurrent, laminal cells papillose to nearly smooth, either similar on both sides of leaf or more strongly convex adaxially than abaxially but then costa percurrent, annulus persistent..... 3.
3. Leaves flaccid when wet, upper laminal cells rectangular, usually epapillose, often adaxially more convex than abaxially...  
..... Barbula sect. Hydrogonium (C. Müll.) K. Saito
3. Leaves firm when wet, upper laminal cells quadrate, papillose, both exposed surfaces similar..... 4.

4. Upper leaf margins usually recurved, propagula (when present) small, of 1-10(15) cells; perichaetial leaves seldom strongly differentiated, with cells mostly parenchymatous..... Barbula Hedw. sect. Barbula
4. Upper leaf margins plane, propagula (when present) often large, of 4-50 or more cells; perichaetial leaves often convolute-sheathing, with cells highly prosenchymatous..... Barbula sect. Convolutae B.S.G.

KEY TO SPECIES AND VARIETIES OF BARBULA AND PSEUDOCROSSIDIUM  
IN NORTH AMERICA

1. Leaves spatulate; upper laminal cells adaxially bulging and abaxially flat, epapillose; costa sharply excurrent; annulus revoluble; U.S.A. (Gulf Coast states), Mexico..... 11. B. agraria Hedw.
1. Leaves lanceolate to ligulate or ovate; upper laminal cells superficially similar on both sides of leaf, or adaxially more strongly convex than abaxially but then costa percurrent, usually papillose, seldom smooth or nearly so; costa ending variously; annulus persistent..... 2.
  2. Upper laminal cells often lax, quadrate to rectangular, usually not or weakly papillose, leaves rather flaccid when wet..... 3.
  2. Upper laminal cells firm, quadrate, usually distinctly papillose, leaves usually firm when wet..... 4.
3. Leaves ovate-lanceolate, margins usually plane, laminal cells 11-15  $\mu$ m wide, 1(-2):1; U.S.A. (southcentral and southwestern states), Mexico..... 9. B. ehrenbergii (Lor.) Fleisch.
3. Leaves narrowly lanceolate to long-triangular, margins narrowly recurved to near apex, laminal cells 8-12  $\mu$ m wide, 1-2:1; Mexico..... 10. B. arcuata Griff.
  4. Abaxial costa surface doubly prorulose (i.e. with both ends of rectangular superficial cells protruding) near apex, often with coarsely mamilllose or very rough appearance; leaf base not sheathing; Canada (Alberta), U.S.A. (southeastern and southwestern states), Mexico..... 5. B. indica (Hook.) Spreng.
  4. Abaxial costa surface with hollow or solid papillae or epapillose, seldom distinctly prorulose near apex (but then leaf base is strongly sheathing), leaf base occasionally sheathing..... 5.

5. Leaf apex acute to somewhat blunt, margins plane or weakly recurved below..... 6.
5. Leaf apex rounded, margins plane to revolute (apex occasionally acute but then margins recurved above midleaf)..... 8.
  6. Costa stoutly short-excurrent, leaf base sheathing; propagula usually present, axillary; Canada (Northwest Territories), U.S.A. (Alaska, Arizona)..... 6. B. amplexifolia (Mitt.) Jaeg.
  6. Costa 1-6 cells subpercurrent, leaf apex entire or occasionally apiculate by a clear or weakly papillose conical cell, leaf base not sheathing; propagula often present, borne on basal rhizoids..... 7.
7. Perichaetial leaves acute to abruptly subulate, loosely sheathing; western Canada, western U.S.A. south to Texas..... 8. B. eustegia Card. & Thér.
7. Perichaetial leaves obtuse to broadly acute, convolute-sheathing; Canada, U.S.A., Mexico..... 7a. B. convoluta Hedw. var. convoluta
  8. Leaves muticous..... 9.
  8. Leaves apiculate, mucronate, or awned..... 12.
9. Leaf margins plane or recurved to midleaf, propagula multicellular..... 10.
9. Leaf margins recurved to near apex, propagula unicellular... 11.
  10. Propagula borne on basal rhizoids, leaves ligulate to oval, costa usually subpercurrent by 4-8 cells; Canada, U.S.A.. Mexico..... 7a. B. convoluta Hedw. var. convoluta p.p.
  10. Propagula borne in upper leaf axils, leaves oval, costa subpercurrent by 2-4 cells; Canada (Northwest Territories), U.S.A. (Alaska).. 7b. B. convoluta var. gallinula Zander
11. Leaves ovate, marginal cells not differentiated as a border; propagula common, yellow-brown, borne in axillary masses; U.S.A. (North Carolina), Mexico..... 4. B. inaequalifolia Tayl.
11. Leaves ligulate, marginal cells often thick-walled in 2-3 rows; propagula uncommon, red-brown, few in leaf axils; Mexico..... 3. B. calcarea Thér.



12. Leaves short-awned; U.S.A. (southwestern states), Mexico..... 14. P. aureum (Bartr.) Zander
12. Leaves apiculate or mucronate..... 13.
13. Leaf margins plane or weakly recurved below midleaf; Canada, U.S.A., Mexico... 7a. B. convoluta Hedw. var. convoluta p.p.
13. Leaf margins recurved to spiral-revolute, usually to near apex..... 14.
14. Costa with adaxial stereid band distinct; leaf margins narrowly recurved, marginal cells not differentiated.. 15.
14. Costa usually lacking adaxial stereid band; leaf margins broadly recurved to spiral-revolute, cells often weakly papillose on exposed portions of margins, and thin-walled, highly chlorophyllose within the spiralled portion.... 16.
15. Leaf apex obtuse to broadly acute, margins recurved in lower 1/2-2/3; propagula apparently not produced in nature; Canada, U.S.A., Mexico..... 1. B. unguiculata Hedw.
15. Leaf apex abruptly rounded to emarginate, margins recurved to near apex; propagula spherical, in leaf axils; Mexico..... 2. B. orizabensis C. Müll.
16. Leaf margins strongly recurved to once (seldom more) revolute, propagula occasionally present on adaxial surface of costa, inner perichaetial leaves convolute-sheathing; Canada (British Columbia, Yukon and Northwest Territories), U.S.A. (Oregon, California)..... 12. P. revolutum (Brid. in Schrad.) Zander
16. Leaf margins strongly spiral-revolute, propagula absent, inner perichaetial leaves not or little differentiated; U.S.A. (southwestern states), Mexico..... 13. P. replicatum (Tayl.) Zander

BARBULA Hedw., Spec. Musc. 115. 1801, nom. cons.

Type species: Barbula unguiculata Hedw. (lectotype fide Steere, 1938).

The genus Barbula is commonly distinguished from Tortula Hedw. by the presence of two stereid bands in its costa rather than only one. However, the adaxial stereid band is often absent in certain species of Barbula. In such cases, the presence of a differentiated epidermis of large-lumened or at least larger-sized cells on the abaxial surface of the costa will distinguish Barbula species. Such an epidermis is not or is only poorly differentiated in Tortula. The North American taxa of Barbula are distinctive and fairly easy to identify by diagnostic characters, although some of the species are polymorphic.

BARBULA Hedw. sect. BARBULA

Synonyms: Barbula sect. Unguiculatae B.S.G., Bryol. Eur.

2: 80. 1842 (fasc. 13-15 Mon. 18) (nom. illeg. incl. typ. gen.). — Barbula sect. Eubarbula C. Mill., Syn.

Musc. 1: 623. 1849 (nom. illeg.). — Barbula sect.

Senophyllum C. Mill., Syn. Musc. 1: 606. 1849 (nom. illeg. incl. typ. gen.). — Barbula sect. Helicopogon (Mitt.)

Chen, Hedwigia 80: 215. 1941 (nom. illeg. incl. typ. gen.).

Additional synonymy is given by van der Wijk, et al. (1959-1969).

Sect. Barbula is characterized by firm leaves; upper leaf margins generally narrowly recurved, occasionally plane; laminal cells papillose; perichaetial leaves seldom strongly differentiated; and, propagula (when present) small, each composed of 1-10(15) cells.

1. Barbula unguiculata Hedw., Spec. Musc. 118. 1801.

Synonymy is given by Podpěra (1954), Saito (1975) and Steere (1938).

This well-known, common species of ruderal habitats is described and illustrated by most authors of moss identification manuals for temperate zone areas. Barbula unguiculata fo. propagulosa Crum is a synonym of B. indica, q.v. I agree with Cardot (1899) and subsequent authors that Barbula stricta Hedw., Spec. Musc. 119, 1801 (type: U.S.A., Pennsylvania, Muehlenberg s.n., G—holotype) is a synonym of B. unguiculata.

This species is readily distinguished from the similar *B. indica* by the usually stoutly mucronate costa, which has scattered simple papillae abaxially above midleaf, and the leaf margins more strongly recurved. *Barbula unguiculata* is rare in Mexico, apparently replaced by the closely related *B. orizabensis*.

Propagula have never been observed in herbarium collections of *B. unguiculata*, although occasional swollen ends of rhizoids ("galls" fide Whitehouse, 1973) may mimic rhizoidal propagula (= "tubers" or "brood bodies"). However, specimens cultivated on nutrient agar by D.V. Basile at NY and on moistened perlite by myself at BUF have produced unicellular, green or brown, elliptical propagula, each ca. 20-25  $\mu$ m long, borne in clusters of uniseriate chains on the ends of long, brown rhizoids arising from the bases of the stems.

2. *Barbula orizabensis* C. Mill., Linnaea 38: 638. 1874.

Type: Mexico, Veracruz, Orizaba, Mohr, 1874 (NY--topotype).

Synonyms: *Barbula recurvicauspis* C. Mill., Bull. Herb. Boiss.

5: 557. 1897. Type: Jamaica, Bridge Hill, Harris 11038 (BM--lectotype), Contenti Road, Harris 10082 (BM--syntype).

*Barbula stenotheca* Ther., Smiths. Misc. Coll. 85(4): 21. 1931, syn. nov. Type: Mexico, Distrito Federal, Río Frío, Amable 1726 (PC--holotype).

*Barbula orizabensis* is easily distinguished from *B. unguiculata* by the characters in the key, although I agree with Theriot (1931) that the two species are closely related. It is described and illustrated by Bartram (1949) and is known from many states in Mexico (Crum, 1951) and from Guatemala (Bartram, 1949) and Jamaica (Crum & Bartram, 1958). It occurs on soil or rock, usually at high elevations. The synonym *B. stenotheca* was described as a species of *Barbula* sect. *Streblotrichum* (= sect. *Convolutae*) on account of the convolute-sheathing perichaetial leaves of the type specimen. Species of sect. *Barbula* occasionally have rather differentiated perichaetia while those of sect. *Convolutae* occasionally have undifferentiated perichaetia. On the basis of evaluation of all characters ("Summe der Merkmale" of Loeske, 1910), however, *B. orizabensis* belongs in sect. *Barbula*.

3. *Barbula calcarea* Thér., Smiths. Misc. Coll. 85(4): 20. 1931.

Type: Mexico, Distrito Federal, Desierto, Amable 1620 (PC--lectotype, NY--isotype); Michoacán, Morelia, Loma Santa María, Arsène 4891 (PC--syntype).

Synonym: *Barbula linguaeifolia* Bartr., Bryologist 50: 204. 1947, syn. nov. Type: Guatemala, Suchiate, Finca El Naranjo, Svihla 2879a (FH--holotype).

Barbula calcarea was described and illustrated by Theriot (1931) and, as B. linguaefolia, by Bartram (1949). This species is closely related to B. inaequalifolia, from which it differs by the characters in the key. The upper leaf margins are occasionally bistratose in small patches and the perichaetial leaves convolute-sheathing in the lower 1/3-2/3. The original description of the synonym B. linguaefolia is incorrect in ascribing plane margins to the type. Propagula were seen only in the lectotype and syntype of B. calcarea. These were found, unattached, in leaf axils, 2-4 per axil, not borne in massive axillary clumps as in B. inaequalifolia. I have seen collections of B. calcarea from Mexico (Distrito Federal, Mexico, Michoacán) and Guatemala; these occurred on soil or calcareous rock at 2600-2800 m elevation.

4. Barbula inaequalifolia Tayl., London Jour. Bot. 5: 49. 1846.  
Type: Ecuador, Jameson, 1863 (FH--isotype).

For complete synonymy see Zander (1968).

A description and illustrations were given by Zander (1968), who cited specimens from U.S.A. (North Carolina), Colombia, Ecuador, China, and Java. An additional station has been noted (Zander, 1976) in Chiapas, Mexico. The following collections extend the geographic range of this species: Mexico: Mexico, between Mexico and Puebla, Dull, 1966 (BUF); Michoacan, Uruapan, Frye & Frye 3051a (TENN); Panama: Chiriqui, Volcan Baru, Pineda 964 (MO); Venezuela: Trujillo, Bocono, Paramo de Guirigay, Lopez & Rodriguez 8788-a (FLAS); India: Uttar Pradesh, Kumaun, Debidhura, Pithoragarh, Srivastava 4348 (BUF). The habitat includes roadsides, banks, paramos, on soil, rock, walls, from 700-3100 m elevation. Husnotiella revoluta Card. occasionally has axillary masses of unicellular propagula (Bartram, 1926; Zander, 1977) and when sterile may be confused with B. inaequalifolia. The former species differs in the following combination of characters states: leaves short-oval to deltoid oval, laminal cell walls evenly thickened, laminal papillae solid, low, broad, simple to multiplex, usually lens-like, and costa with only one stereid band.

In spite of the peristome being red, well developed and twisted 1-4 turns, B. inaequalifolia may be better placed in Bryoerythrophyllum Chen because of its red coloration and closely hollow-papillose, thin-walled upper leaf cells. It has much the same general appearance as does Bryoerythrophyllum bolivianum (C. Müll.) Zander, which, however, has plane margins, lacks propagula, and has the rudimentary peristome typical of Bryoerythrophyllum species (Zander, 1978b). This is another confounding example of a moss species with a gametophyte matching the characters of one genus and a sporophyte those of another.

BARBULA sect. CONVOLUTAE B.S.G., Bryol. Eur. 2: 91. 1842 (fasc. 13-15 Mon. 29). Lectotype: Barbula convoluta Hedw.

Synonyms: Streblotrichum P. Beauv., Mag. Enc. 5: 317. 1804. — Barbula sect. Streblotrichum (P. Beauv.) Limpr., Laubm. Deutsch. 1: 626. 1888. — Barbula subg. Streblotrichum (P. Beauv.) K. Saito, Jour. Hattori Bot. Lab. 39: 499. 1975. Type: Barbula convoluta Hedw.

This section is distinguished by the combination of the following character states: leaves firm when wet; plane or weakly recurved leaf margins; papillose laminal cells; adaxial stereid band of costa usually distinct; perichaetial leaves usually convolute-sheathing; and, propagula (when present) often large, composed of 4-50 or more cells.

5. Barbula indica (Hook.) Spreng. in Steud., Nomencl. Bot. 2: 72. 1824. [Sensu amplo.]

Basionym: Tortula indica Hook., Musci Exot. 2: 135. 1819, nom. nov. for Trichostomum indicum Schwaegr., Spec. Musc. Suppl. 1(1): 142, 1811, hom. illeg. non Trichostomum indicum Willd. ex Schrad., 1803. Type: India, Madras, Tranquebar, Röttler s.n. (NY—isotype).

Synonyms: Trichostomum orientalis Web., Arch. Syst. Naturgesch. 1(1): 129. 1804. — Barbula orientalis (Web.) Broth., Nat. Pfl. 1(3): 403. 1902, non B. orientalis Brid., 1819. — Semibarbula orientalis (Web.) Wijk & Marg., Taxon 8: 75. 1959.

Barbula cruegeri Sond. ex C. Müll., Syn. Musc. 1: 618. 1849, syn. nov. Type: Trinidad, La Ventille, Crueger, 1846 (SPA—isotype).

Tortula gregaria Mitt., Jour. Linn. Soc. Bot. London Suppl. 1: 29. 1859, syn. nov. Type: Nepal, Tambar R., Hooker 166 (NY—syntype). — Barbula gregaria (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1871-72: 424. 1873 (Ad. 1: 272).

Barbula erosa Hampe in C. Müll., Bot. Zeit. 20: 348. 1862, syn. nov. Type: Venezuela, Baruta, Trumpff, 1857 (BM—isotype).

Barbula rufipes Schimp. ex Besch., Mém. Soc. Nat. Sci. Nat. Cherb. 16: 180. 1872, syn. nov. Type: Mexico, Veracruz, Orizaba, Mueller, 1853 (BM—holotype). — Semibarbula rufipes (Schimp. ex Besch.) Hilp., Beih. Bot. Centralbl. 50(2): 622. 1933.

Barbula cancellata C. Müll., Flora 56: 483. 1873.



- Barbula wrightii Sauerb. in Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78: 409. 1880 (Ad. 2: 673), syn. nov., nom. nov. for Barbula obscura Sull., Proc. Amer. Acad. Arts Sci. 5: 277. 1861, non B. obscura Mitt., 1859. Type: Cuba, Wright 31 (BM, NY--isotypes). -- Tortula obscura (Sull.) Mitt., Jour. Linn. Soc. Bot. 12: 150. 1869.
- Barbula purpuripes C. Müll., Bull. Herb. Boiss. 5: 558. 1897, syn. nov. Type: Jamaica, Cinchona, Harris 11022 (BM, NY--isotypes).
- Barbula microglottis C. Müll., Hedwigia 37: 232. 1898, syn. nov. Type: Haiti, "Cape Haytien," Eggers, 1887 (NY--isotype).
- Barbula hypselostegia Card., Rev. Bryol. 36: 84. 1909, syn. nov. Type: Mexico, Puebla, Honey Station, Pringle 10653 (PC--holotype, TENN--isotype). -- Streblotrichum hypselostegium (Card.) Hilp., Beih. Bot. Centralbl. 50(2): 635. 1933.
- Barbula muenchii Card., Rev. Bryol. 36: 84. 1909, syn. nov. Type: Mexico, Chiapas, San Cristóbal, Muench, 1907 (NY--isotype).
- Barbula pringlei Card., Rev. Bryol. 36: 85. 1909, syn. nov. Type: Mexico, Morelos, Cuernavaca, Pringle 10637 (PC--lectotype, BM, FH, TENN--isotypes), 15177 (PC--syntype). -- Streblotrichum pringlei (Card.) Hilp., Beih. Bot. Centralbl. 50(2): 635. 1933.
- Hyophila uliginosa E.G. Britt., Bull. Torrey Bot. Cl. 42: 4. 1915. Type: St. Jan, Bethania, Britton & Shafer 367 (NY--holotype).
- Barbula unguiculata fo. propagulosa Crum, Bryologist 72: 241. 1969, syn. nov. Type U.S.A., Tennessee, Montgomery Co., Clebsch 581 (MICH--holotype).
- Barbula horrinervis K. Saito, Jour. Hattori Bot. Lab. 39: 486. 1975, syn. nov. Type: Japan, Tokyo, Okutama, Saito 4936 (MICH--isotype).

Additional synonymy is given by Crum and Steere (1957), Saito (1975) and Steere (1938).

Plants turf-forming, yellow-green to brown; stems seldom branching, to 1.2 cm tall, in transverse section pentagonal, central strand distinct, cortex of smaller, darker cells, epidermis not differentiated; axillary hairs usually of 4-8 uniseriate cells, all clear or the basal 1(-2) with somewhat thickened walls and yellow-brown coloration; tomentum absent. Leaves crowded to rather distant, about equal in size from base to apex, when dry incurved-appressed, often infolded above, occasionally catenulate, when wet erect-

spreading, incurved to plane, ovate to ligulate, occasionally lanceolate or long-triangular, 0.5-1.8 mm long, with a deep, narrow groove adaxially along the costa, margins plane to weakly recurved at midleaf, entire; leaf apex somewhat incurved or weakly cucullate to nearly plane, rarely reflexed, rounded to bluntly acute, apiculate by a clear, not or little papillose, conical cell, rarely muticous; leaf base scarcely differentiated to much broadened, square to rectangular or oval, basal margins not or shortly decurrent; costa usually percurrent or ending 1-4 cells below apex or occasionally excurrent in a short, sharp mucro, abaxial superficial cells near apex long- to short-rectangular or quadrate, doubly prorulose (distal and proximal ends of cells protuberant), occasionally nearly smooth or both prorulose and simply papillose, adaxial superficial cells long- to short-rectangular, smooth, or quadrate and papillose in patches above midleaf; costa in transverse section semicircular to elliptical, ventrally flat to convex, lamina inserted at about 90° angle, adaxial epidermis often differentiated as one layer of thin-walled cells, adaxial stereid band absent or weak, guide cells in one layer of 2-4 cells, abaxial stereid band strong, abaxial epidermis undifferentiated or represented by one layer of thick-walled cells with semicircular lumens or with thin walls and circular lumens. Upper laminal cells quadrate, 7-9(10)  $\mu\text{m}$  wide, walls thin to evenly thickened, superficially weakly bulging to conic-protuberant, lumens angular, arranged in a weak pattern of longitudinal rows, papillae low-multiplex, mostly hollow, with 4-8 salients per lumen, occasionally coroniform above strongly protuberant cell walls; basal laminal cells medially smooth, 8-12  $\mu\text{m}$  wide, 2-5:1, rectangular, evenly thickened or thin-walled, usually bordered on the margins by 1-4 rows of short-rectangular cells. Propagula often present, borne on stalks in leaf axils issuing just above the axillary hairs, obovoid, clavate, spindle-shaped, elliptical, or spherical, smooth, colliculate or armed with 1-several short, pointed branches, 70-300  $\mu\text{m}$  long, of 8-50 or more cells, green to brown. Dioicous; perichaetia terminal, leaves ovate, entirely prosenchymatous and convolute-sheathing grading to lanceolate, prosenchymatous only in the lower 1/3 of the leaf and weakly sheathing, 0.8-2.5(3.0) mm long; perigonia terminal on smaller plants, gemmate, leaves oval.

Seta 0.7-1.3 cm long, red-brown, twisted clockwise; urn 0.8-1.8 mm long, red-brown, smooth when dry, elliptical to ovoid, occasionally curved, neck little differentiated, exothecial cells 18-25  $\mu\text{m}$  wide, 3-6:1, thin- or thick-walled, evenly thickened, stomates present at base of urn, phaneropore, annulus weakly differentiated; peristome inserted on mouth of capsule, of 32 teeth weakly fused in 16 pairs, 0.7-1.7 mm long, teeth linear, densely spiculose, red to orange, with many articulations, little to strongly twisted 0.25-3.0 times, counterclockwise; spores (8)9-12  $\mu\text{m}$  in diameter, smooth to weakly papillose, light brown to yellow-brown; operculum 0.8-1.7 mm long, long- to short-conic, cells twisted counterclockwise. Calyptra 2.0-2.2 mm long, cucullate, usually rough apically with prorulose cells.

The habitat of B. indica includes soil, clay, limestone, coral walls, roadbanks, riverbanks, walls, limepit, tree trunks, from near sea level to 3900 m. I have examined specimens from Canada (Alberta), U.S.A. (southeastern and southwestern states and Hawaii), Bermuda, Mexico (Chiapas, Durango, Hidalgo, Jalisco, Morelos, Oaxaca, San Luis Potosí, Sonora, Veracruz), Guatemala, British Honduras, Cuba, Jamaica, Dominican Republic, Haiti, Puerto Rico, St. Lucia, Barbados, St. Jan, New Providence, Martinique, Trinidad, Venezuela, Surinam, Colombia, Peru, Nepal, India, Hong Kong, Japan, Philippines, and New Guinea.

Barbula indica (Fig. 1-14) is a polymorphic species, occurring mainly in tropical and warm temperate areas, and includes a profusion of variants with various permutations of character states. Under this name or its synonyms, it is illustrated and described by Saito (1975) and Steere (1938) among others. On account of the considerable synonymy accepted here, a redescription is given above, based on New World specimens. Certain characters that are usually conservative in other species, e.g. length and degree of twisting of peristome teeth, degree of differentiation of perichactial leaves, size, shape and position of propagula, vary markedly. For this reason, synonyms include combinations in other generic names such as Hydrogonium (C. Müll.) Jaeg., Semibarbula Herz. ex Hilp. and Streblotrichum P. Beauv.

Previous authors have treated the Old World and New World representations as separate entities, although variation is similar throughout the tropics. Saito (1971) reduced certain Asian names to synonyms of the New World B. cruegeri, but later (1975) referred these to B. indica instead. In North America north of Mexico, B. indica has been known under the synonym B. cruegeri, as discussed by Steere (1938). Recently, the checklist of Crum et al. (1973) replaced B. cruegeri (sensu North American authors) with the name B. cancellata, because (H. Crum, pers. comm.) the Texan type of the latter has the small, obovoid propagula characteristic of most collections in North America north of Mexico, while there were indications that B. cruegeri (with a type from Trinidad) represents a different, tropical taxon.

There appear to be two major trends in morphological appearance in B. indica. Barbula indica s. str. has narrowly oval to elliptical leaves, with margins plane or weakly recurved at midleaf, and small, green, obovoid propagula occurring in masses in upper leaf axils. The type from India has propagula 70-90  $\mu$ m long. This expression is found throughout the range of the species. A somewhat different-looking plant in extreme form is B. indica facies "B. gregaria," which was well illustrated by Saito (1975) under the synonym B. horrinervis. This morph has broadly oval leaves with plane margins and massive, brown, elliptical to spherical, many-celled propagula occurring singly or very few together in upper leaf axils. Facies "B. gregaria" is seldom found in temperate areas although it is known from Japan (type of B. horrinervis) and from Canada

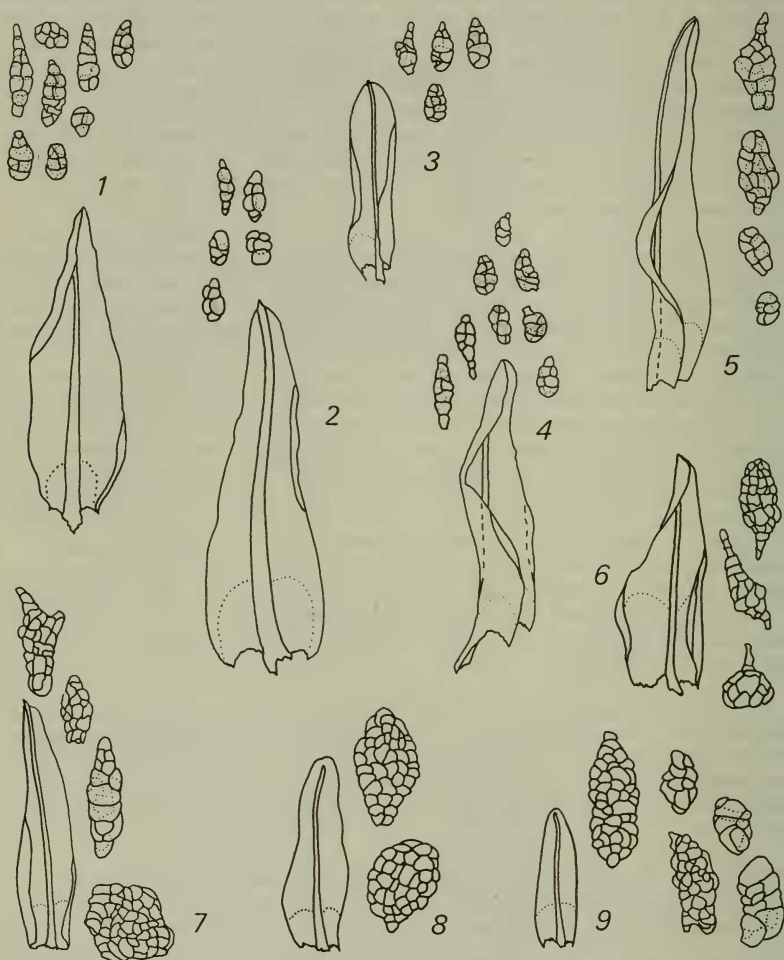
Vitt 24189--ALTA, Horton 15697--ALTA). A third, less distinctive trend that is widespread in the tropics is the production of propagula, these usually massive, on basal rhizoids, but uncorrelated with leaf morphology. Some of these propagula are apparently formed from an apical cell with two cutting faces and are similar to the "bilateral tubercles" of *Leptobryum pyriforme* (Hedw.) Wils. illustrated by Berthier (1978). The type of *B. cruegeri* has elliptical, plane to recurved leaves, and brown tubers borne on rhizoids from lower leaf axils or buried in the soil, ranging from 95-300  $\mu$ m in length, from 15 to many cells in composition, and obovoid, spindle-like, elliptical or spherical in shape, superficially smooth to colliculate (raspberry-like).

Because of considerable intergradation in characters between these variants, infraspecific categories are not recognized. Individual collections were mostly stenomorphic between plants in expression of particular character states. The characters of the propagula were, however, variable within some collections. In certain specimens, massive propagula on basal rhizoids occurred together with either small, obovoid or massive axillary propagula or with intermediate-sized axillary propagula. Saito (1975) illustrated the Japanese synonym *B. horrinervis* as having massive, elliptical, apiculate propagula. In fact, in tropical and subtropical areas worldwide, specimens of *B. indica* may be found with propagula of various sizes and shapes that have one or more apiculi or spines, apically or laterally, resulting in spindle shapes, "ocarina" shapes and "mine" shapes. Saito (1975) also indicated that, in Japan, plants with massive propagula have plane leaf margins (*B. horrinervis*) and those with small propagula have recurved leaf margins (*B. indica*), but this correlation is only poorly reflected on a worldwide basis.

Although intergrading variants that are distinctive in the extreme are often recognized, and although the two major variants of *B. indica* may be biological entities deserving infraspecific scientific names, satisfactory disposition of the multiplicity of taxonomic synonyms following non-discontinuous, non-exclusive criteria (e.g. the "75 percent convention" discussed by Mayr, 1942) is impossible or at least arbitrary, if type methodology is rigorously followed. This is a rather subtle, non-biological, bookkeeping limitation of the Code to practicality of specific and infraspecific concepts.

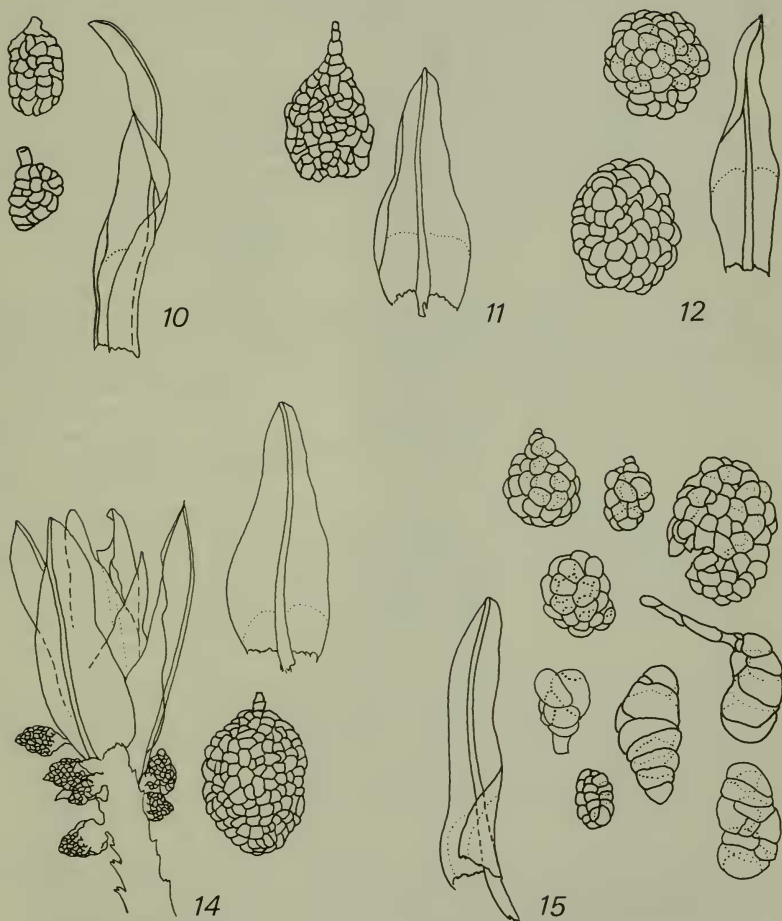
The term "prorula" referring to a protrusion of the distal or proximal ends of superficial cell walls, or of both (doubly prorulose), was coined by Argent (1973) as pointed out by Manuel (1974). Weber and Simone (1977) suggested the term "scindula" for the same feature, and During (1977, p. 15) further discussed this morphological trait. Above midleaf, the abaxial costal surface of *B. indica* is usually distinctly doubly prorulose; however, some specimens may have relatively smooth costal surfaces or be covered with quadrate, hollow-papillose cells. Usually, such collections





Figures 1-14. Variation in leaf and propagulum morphology in *Barbula indica* (Hook.) Spreng. Leaves, X32; propagula (which are axillary unless noted), X82. 1. U.S.A. Kentucky, Zander 4640 (BUF). 2. Mexico: Frye 2143 (NY). 3. Mexico: Richards et al. 629 (FH). 4. Mexico: McGregor 5314 (NY). 5. Venezuela: Griffin & Lopez 415 (FLAS). 6. Venezuela: Dall'Aglia 367 (BUF). 7. Canada: Alberta, Vitt 24189 (ALTA). 8. Cuba: Ekman 8267 (NY). 9. Puerto Rico: Britton 5157 (NY)—mixture of rhizoidal and axillary propagula.





10. Peru: Mexia 62589 (MO). 11. Jamaica: Hermann 22919 (BUF).  
 12. Haiti: Bartlett 17583 (NY). 13. Mexico: Sharp 4665 (FH).  
 14. Trinidad: Crueger, s.n. (SPA--type of *Barbula creugeri*  
 Sond. ex C.Müll.)--axillary and rhizoidal propagula.

may be referred to B. indica by the following combination of gametophyte characters: leaves ligulate to oval, base not sheathing, margins plane or weakly recurved at midleaf, apex rounded-obtuse to bluntly acute, apiculate with a clear cell, upper laminal cells papillose, quadrate, mostly 7-9  $\mu\text{m}$  wide, and costa ending 1-4 cells below apex.

In Leptobryum pyriforme, environmentally triggered switch mechanisms apparently control the formation of the three possible kinds of propagula found in this species (Berthier, 1978). However, variation in propagula size, number, ornamentation and position in B. indica may be genetically based, possibly as the result of selection for certain modes of diaspore dispersal appropriate in different habitats. The small axillary propagula are abundant, usually 50-100  $\mu\text{m}$  long, of 3-6 cells, thin-walled, clavate to spindle-shaped, have few or no internal oil globules, and may be interpreted as an adaptation for colonization through wide dispersal by water and immediate regeneration. However, the massive axillary or rhizoidal propagula are few, usually 100-230  $\mu\text{m}$  long, many-celled (to 50 or more), thick-walled, elliptical to spherical and often branching, have abundant oil and may well be a specialization for very local dispersal or non-dispersal. In the large size, anchoring arms, and position often buried in the soil, massive propagula may be examples of "atelochoy" (van der Pijl, 1972) or "precinctiveness" (Carlquist, 1966, 1974) of diaspores of vascular plants in insular situations. Intermediate-sized propagula are common, however, and many collections lack propagula altogether. That plants of B. indica with numerous, small propagula are typically Temperate Zone in distribution while those with few, large propagula are typically tropical indicates the possibility of a response to a north-south cline in selection for the above features, perhaps corresponding to the temperate and tropic regional differences in r- and K-selection discussed by Pianka (1970). Studies in cultivation and the correlation of propagula size with environmental parameters need to be done before the above suggestions can be considered anything more than hypotheses. Large, buried propagula are found in other species of Barbula sect. Convolutae as well as elsewhere in the Pottiaceae and in other moss families (Whitehouse, 1966, 1976).

There are several additional regional variants with unusual or locally stenotypic character states that may be geographic races. Two collections from Canada (Alberta: Vitt 24184--ALTA, Horton 15697--ALTA) are geographically isolated, have massive elliptical propagula in the upper leaf axils and all leaves are mucicous, lacking the characteristic clear apiculus; however, many plants of the type of the synonym B. hypselostegia, from Mexico, match those of the Albertan collections exactly. Some specimens that I have seen from India have unusually thin, collapsed leaf cell walls that do not regain their original shapes after thorough wetting. Most specimens from the Philippines have the abaxial costal surface extremely rough with strongly protruding prorulae. Many collections

from the West Indies show an unusual development of an epidermis of sub-quadrate, hollow-papillose cells on the distal abaxial surface of the costa; others have leaves that are long-ligulate and have capitulate, massive laminal papillae. These variants are not given infraspecific names because of abundant intergradation of character states and because most would be necessarily based on "one-character taxonomy," which I eschew.

Anoetangium aestivum (Hedw.) Mitt. when sterile may be confused with forms of B. indica; however, in the former the leaf base is usually poorly differentiated, the costa has only one stereid band and abaxial prorulae are lacking.

6. *Barbula amplexifolia* (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. ~~1871-72: 424. 1873.~~

Basionym: *Tortula amplexifolia* Mitt., Jour. Linn. Soc. Bot. Suppl. 1: 29. 1859. Type: India, Uttar Pradesh, Kumaun, western Himalayas, Strachey & Winterbottom 15/37 (NY--holotype).

Synonyms: *Hydrogonium amplexifolium* (Mitt.) Chen, Hedwigia 80: 240. 1941.

*Barbula haringae* Crum, Southw. Naturalist 1(1): 36. 1956, syn. nov. Type: U.S.A., Arizona, Cochise Co., Huachuca Military Reserve, Goodding Cry. 85 (Haring 10000) (CANM--holotype, MICH--isotype); South Huachuca Game Preserve, Goodding Cry. 285 (Haring 10285a), Goodding Cry. 293 (Haring 10293) (CANM--paratypes).

*Barbula amplexifolia* has been described and illustrated by Gangulee (1972) as *Hydrogonium amplexifolium* and by Crum (1956) as *B. haringae*. *Barbula corensis* (Card.) K. Saito, described and illustrated by Saito (1975), is doubtfully distinct. In addition to the type specimens of the synonym *B. haringae* that were reported from Arizona by Crum (1956) and the arctic Alaska collection reported as *B. corensis* (det. R. Zander) by Steere (1978), the following collections represent the known New World distribution: Canada: Northwest Territories, District of Mackenzie, Liard Range, 12.8 km SW of Mt. Flett, 60° 34'N, 123° 45'W, Vitt 20521 (ALTA); Nahanni National Park, South Nahanni R., Virginia Falls, 61° 38'N, 125° 42'W, Steere 76-605 (NY); U.S.A.: Alaska, Chandalar Quad., Yukon R.-Prudhoe Bay Haul Rd., Wiehl Mt., 67° 39'N, 149° 40'W, Murray 76-691B (ALA). The habitat includes mountain slopes, wet limestone cliffs, tundra, on or under damp rocks, mist zone of waterfall, at 760-1800 m elevation.

The short-ovoid to nearly spherical propagula of *B. amplexifolia* are found in masses in the leaf axils. The propagula are similar in and between most collections in the red-brown coloration and the size, usually 40-90 µm long. However, the very ample

collection Steere 76-605, which includes many small sods, has propagula generally similar within each sod but heterogeneous between sods, grading from the normal size in some sods up to 150  $\mu$ m long, short-elliptical, mostly only 3-4 in each axil, in other sods. Plants of sods with unusually large propagula have broader leaves than usual, these ovate-triangular, and approach the morphology of B. convoluta var. gallinula (see below). Plants of this latter taxon may also be found in this collection and hybridization may be the cause of intergradation in propagula characters in the Virginia Falls station; however, sporophytes of neither B. amplexifolia nor B. convoluta var. gallinula have been seen in the New World. A more probable explanation might be a plastic response on the part of certain sods of B. amplexifolia to unusual environmental factors, but there is no evidence at present to support this.

The abaxial costal surface is usually smooth in B. amplexifolia but in some specimens double prorulae similar to those of B. indica may be found. The former species differs from the latter in the stout costa, which is commonly short-excurrent, the sheathing leaf base and the propagula borne only in the leaf axils, subspheric, red-brown, and usually 40-90  $\mu$ m long.

7a. Barbula convoluta Hedw. var. convoluta, Spec. Musc. 120. 1801.

Synonyms: Tortula convoluta (Hedw.) Gaertn., Meyer & Scherb., Oek. Techn. Fl. Wetterau 3(2): 92. 1802. — Streblotrichum convolutum (Hedw.) P. Beauv., Prodr. 89. 1805.

Additional synonymy is given by Podpera (1954) and Steere (1938).

Barbula convoluta is a well-known, common, widely distributed, Temperate Zone species described and illustrated by Saito (1975), Steere (1938) and others. The shape of the leaf apex is quite variable. It is known from Mexico from a single report from southern Baja California (Koch & Crum, 1950). Spherical to elliptical, red-brown multicellular propagula, often massive, are found on rhizoids buried in the soil in most collections. Rhizoidal propagula are seldom mentioned in descriptions although illustrated for B. convoluta by Hilpert (1933), Moenkemeyer (1927) and Wilczek & Demaret (1976). When present, such propagula allow this species to be distinguished with ease from the similar B. unguiculata, in which propagula have never been found in nature.

7b. Barbula convoluta var. gallinula Zander, var. nov.

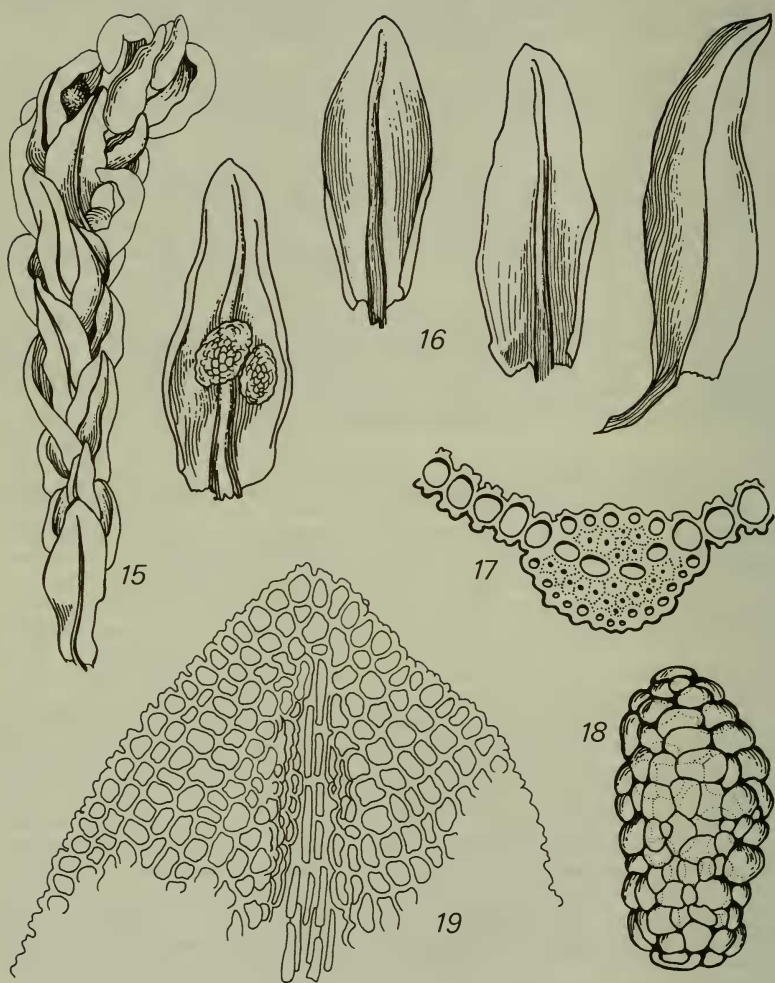
Varietati typicae similis, sed propagulis portatis in pedicellis intra axillas foliorum superiorum differt; folia ovalia, costis terminantibus in 2-4 cellulas sub apicibus foliorum.

Similar to the typical variety but differing by the propagula being borne on stalks in the axils of the upper leaves; leaves oval, with costae ending 2-4 cells below the leaf apices.

Type: Canada: Northwest Territories, District of Mackenzie, Nahanni National Park, South Nahanni R., Virginia Falls, 61° 38'N, 125° 42'W, Scotter 22432, 3 Sept. 1974 (NY--holotype; BUF--isotype). Paratypes: Canada: same locality, Scotter 22408 (NY), Steere 76-605 p.p. (NY); South Nahanni R., Kraus Hot Springs, 61° 15'N, 124° 03'W, Steere 76-290 p.p. (ALA); U.S.A.: Alaska, Survey Pass Quad., confluence of Altna and Nahtuk Rivers, 67° 25'N, 153° 43'W, Murray 5067c (ALA); Philip Smith Quad., Yukon R.-Prudhoe Bay Haul Rd., W end of Atigun Canyon, 68° 27'N, 149° 18'W, Murray 77-228 (ALA); Harrison Bay Quad., National Petroleum Reserve-Alaska, Fish Creek Test Well 1, 70° 19'N, 151° 58'W, Murray 77-813B (ALA).

Barbula convoluta var. gallinula (Fig. 15-19) is known only from sterile plants in alpine-montane areas of northwestern North America. The plants are not common where found and grow gregariously or as small sods on rock--mainly limestone--or soil, in lowland tundra slopes, on cliffs, or mist areas of waterfalls, from near sea level to 400 m elevation. The new variety differs from var. convoluta in the characters cited in the diagnosis above. Under the dissecting microscope, the egg-shaped propagula are easily visible in the axils of the leaves of wet or dry plants. The general appearance of the plants is reminiscent of poultry, whence the name. The axillary propagula are red-brown, spherical or elliptical, massive, 120-250 µm long, lacking apiculi or spines but otherwise similar to the propagula of facies "B. gregaria" of B. indica. There appears to be morphological and geographical discontinuity in the characters of propagula position in B. convoluta while no clear, similar discontinuity can be discerned in B. indica. Because B. indica with large axillary propagula has also been found in Canada, it is necessary to carefully determine the presence of simple papillae (not prorulae) on the abaxial costal surface. In addition, the leaf cells of B. convoluta var. gallinula are 9-12 µm wide, as opposed to 7-9(10) µm for B. indica. Barbula convoluta var. gallinula consistently has oval leaves; the var. convoluta occasionally may have oval leaves but usually such specimens have the costa ending 4-6 cells below the leaf apex. Barbula amplexifolia c.v. may approach B. convoluta var. gallinula closely in size of the propagula and in unusual, broadly deltoid leaves when both occur at the same station.





Figures 15-19. Barbula convoluta var. gallinula Zander.  
15. Gametophore, X32. 16. Leaves, X46. 17. Costal transverse section near midleaf, X320. 18. Axillary propagulum, X320. 19. Leaf apex, X320.

The European *Barbula convoluta* var. *propagulifera* Glow. (Yugoslavia: Soca Tal, Kanal, Glowacki, 1909, GJO--holotype) is a new synonym of *Gymnostomum aeruginosum* Sm. The type corresponds to the facies "*G. calcareum*" and has small, clavate, axillary propagula (see discussion by Zander, 1977).

8. *Barbula eustegia* Card. & Ther., Bot. Gaz. 30: 17. 1900.

Type: U.S.A., Idaho, Latah Co., Cedar Creek, Henderson 4231 (NY--isotype). [Columbariate.]

Synonym: *Barbula whitehouseae* Crum, Southw. Naturalist 1(1): 35. 1956, syn. nov. Type: U.S.A., Texas, Fannin Co., Lake Crockett, ca. 19 km N of Honey Grove, Whitehouse 21001 (CANM--isotype); Tarrant Co., Eagle Mountain Lake, Whitehouse 17984 (CANM--isoparatype).

For additional synonymy, see Steere (1938).

This species was described and illustrated by Flowers (1973), Lawton (1971) and Steere (1938). It is known from Washington, Idaho, Montana, Utah and Texas in the U.S.A. and was reproted from British Columbia, Canada, by Crum (1965). Androgametophores are usually not noted in descriptions of *B. eustegia*. These are smaller than the gynogametophores and mixed with them, and are often minute, largely buried in the soil, with perigonia terminal (singly or paired). Propagula, similar to those of *B. convoluta*, are present on basal rhizoids in the soil in most specimens including the types of *B. eustegia* and *B. whitehouseae*. Both of these type collections, also, have apiculate leaf apices, and the lack of the apiculus is not a good character state for distinguishing *B. eustegia* from *B. convoluta* though indicated as such by some authors. *Barbula eustegia* apparently differs from *B. convoluta* only in the appearance of the perichaetial leaves (see key) and in its largely western distribution. It may better be recognized as a variety of *B. convoluta* (if at all) but is here presented as a "columbariate" (pigeonhole) species (cf. Zander, 1978a) pending further study. Crum (1965) and Steere (1938) considered *B. eustegia* to be closely related to the European *B. flavipes* B.S.G. (= *B. enderesii* Garov.). The perichaetial leaves of the latter species are far larger and more strongly differentiated in the specimens I have seen than are those of *B. eustegia*. However, there is probably a close relationship—Moenkemeyer (1927) pointed out that the propagula of both *B. convoluta* and *B. flavipes* are similar in morphology and rhizoidal position.

BARBULA sect. HYDROGONIUM (C. Müll.) K. Saito, Jour. Hattori Bot. Lab. 39: 492. 1975.

Basionym: Trichostomum sect. Hydrogonium C. Müll., Linnaea 40: 297. 1876. Type species: Barbula ehrenbergii (Lor.) Fleisch. (lectotype by Saito, 1975).

Synonyms: Hydrogonium (C. Muell.) Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78: 405. 1880. -- Barbula subg. Hydrogonium (C. Müll.) Fleisch., Musci Fl. Buitenzorg 1: 352. 1904.

This taxon is distinguished from the other sections of Barbula subg. Barbula by the leaves lax when wet; upper leaf margins plane to narrowly recurved, laminal cells usually rectangular, epapillose or seldom weakly papillose, their surfaces often adaxially more strongly convex than abaxially; the perichaetial leaves often convolute-sheathing; and, propagula often present, usually stellate and brown to green in color.

9. Barbula ehrenbergii (Lor.) Fleisch., Musci Arch. Indic. Exs. ser 4: n. 161. 1901. [Columbariate.]

Basionym: Trichostomum ehrenbergii Lor., Abhandl. Akad. Wiss. Berlin 1867: 25. 1868.

Synonym: Barbula ehrenbergii var. mexicana Ther., Smiths. Misc. Coll. 85(4): 19. 1931, syn. nov. Type: Mexico, Nuevo Leon, Monterrey, Abbon 10969 (PC--holotype).

For additional synonymy, see Podpera (1954).

Description and illustration of B. ehrenbergii has been given by Flowers (1973) and Steere (1938), among others. This species intergrades with B. arcuata in Mexico and Central America; some collections (e.g. Belize: Big Falls, Lundell, 1965--NY) are quite impossible to assign to either species. In the New World, B. ehrenbergii is largely a Temperate Zone species, while B. arcuata is restricted to the West Indies, Mexico, Central America, and areas of South America. The leaves of the former are more commonly papillose (albeit weakly so) than are those of the latter. Nonetheless, the two should be considered columbariate species until an intensive study can be made of their relationship.

Barbula abbonii Ther. (Mexico: Nuevo Leon, Monterrey, Abbon 10970, PC--holotype) is referred to B. ehrenbergii by Crum (1951); however, the tubulose, relaxed leaves with broadly decurrent basal margins and yellow-brown upper laminal cells, lead me to believe that it is a synonym of Didymodon tophaceus (Brid.) Lisa.

Barbula ehrenbergii is reported (Crum, 1951; Flowers, 1973; Steere, 1938) in North America from the U.S.A. in Missouri, Texas, Oklahoma and Utah, and from Mexico in Coahuila, Nuevo León and San

Luis Potosi. I have also seen a Mexican collection from Chihuahua, Sta. Elena Canyon of Rio Grande, Fern Canyon, 29° 09'N, 103° 39'W, Wendt & Lott 101 (TEMN). In other areas of the New World it is known from Belize (Steere, 1934) and Cuba (Theriot, 1939-1941; Welch, 1950). I agree with Crum and Steere (1958) that the report of this species from Haiti (Theriot, 1944) was based on a specimen (PC!) that is actually Hymenostylium recurvirostrum (Hedw.) Dix. The habitat of B. ehrenbergii is wet rocks, usually calcareous, often in springs or running water, often tufa-forming.

Barbula ehrenbergii (Lor.) Fleisch. is indicated to be an illegitimate homonym in the Supplement (Volume 5) of Index Muscorum (van der Wijk, 1959-1969). However, the supposed earlier name was apparently only a misspelling of B. ehrenbergiana on the part of Kindberg (1888-1891) and is not listed in Steere and Crum's (1977) catalogue of Kindberg's new combinations and new taxa.

10. Barbula arcuata Griff., Calcutta Jour. Nat. Hist. 2: 491. 1842.  
Type: India, Griffith 27 (BM—holotype). [S. ampl. & columb.]

Synonyms: Hydrogonium arcuatum (Griff.) Wijk & Marg., Taxon  
7: 289. 1958.

Barbula subulifolia Sull., Proc. Amer. Acad. Arts Sci. 5: 227.  
1861, syn. nov. Type: Cuba, Wright 32 (BM—isotype). —  
Tortula subulifolia (Sull.) Mitt., Jour. Linn. Soc.  
Bot. 12: 161. 1869.

Barbula crispula Hampe in Jaeg., Ber. S. Gall. Ges. 1871-72:  
438. 1873 (Ad. 1: 286), syn. nov. Type: Cuba: Wright 27  
(BM—holotype).

Barbula macrogonia Besch., Jour. de Bot. 8: 61. 1894, syn. nov.  
Type: Guadeloupe, Baines Jaunes, Marie s.n. (BM—isotype).

Barbula suberythropoda C. Mull., Bull. Herb. Boiss. 5: 194.  
1897, syn. nov. Type: Guatemala, Alta Vera Paz, Pansamala,  
Tuerckheim, 1887 (BM, NY—iso-types).

Barbula ferrinervis C. Mull., Bull. Herb. Boiss. 5: 557. 1897,  
syn. nov. Type: Jamaica, Bridge Hill, Harris 11026 (BM,  
NY—iso-types).

Barbula ferrinervis var. eggersiana C. Muell., Hedwigia 37: 232.  
1898, syn. nov. Type: Santo Domingo, Rio Camu, Eggers 2685  
(June 1887) (BM—isotype). — Barbula eggersiana (C. Mull.)  
C. Mull., Gen. Musc. Frond. 437. 1900.

Trichostomum setifolium C. Mull., Hedwigia 37: 234. 1898,  
syn. nov. Type: Puerto Rico, Sabana, Sintensis, 1886  
(BM, NY--isotypes). -- Barbula setifolia (C. Mull.)  
Broth., Nat. Pfl. 1(3): 408. 1902.

Barbula stillicidiorum Card., Rev. Bryol. 37: 126. 1910, syn.  
nov. Type: Mexico, Veracruz, Barnes & Land, 1906 (NY--  
isotype).

Barbula rubricaulis Ther., Smiths. Misc. Coll. 85(4): 19. 1931,  
syn. nov. Type: Mexico, Nuevo Leon, Monterrey, Abbon  
10968 (FH--isotype).

For additional synonymy, see Gangulee (1972) and Saito (1975).

Barbula arcuata is known in the Old World from India, Burma, Malaysia, Indonesia, Molucca, New Guinea, the Philippines, China, Japan and western Oceania. It has been well described and illustrated by Gangulee (1972) and Saito (1975). Its New World distribution is similarly tropical and subtropical. I have seen material from Mexico (Nuevo Leon, Veracruz), Guatemala, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Guadeloupe, and Venezuela. Steere (1948) reported it, as the synonym B. subulifolia, from Ecuador. Judging from the checklist of Pursell (1973), I here report this species as new to Venezuela: Miranda, between Los Ocumites tunnel and Cortada de Maturín highway (Caracas-Valencia), Ramírez Cr 46-74 (TENN). The habitat includes wet cliffs, riverbanks, calcareous soil, wet rock, travertine, at 150-1350 m elevation.

As is common in hygrophytes, Barbula arcuata is polymorphic. The leaf shape is especially variable; some forms approach the broad-elliptical leaves of B. ehrenbergii and other forms, these mainly in the West Indies, have very narrow, subulate leaves, such as in the types of B. ferrinervis or B. setifolium, synonyms. The terminal perigonia may be visually accentuated in plants with very narrow leaves (e.g. the type of the synonym B. macrogonia). Multicellular, green, fusiform to stellate propagula are commonly present, borne on branching stalks in the leaf axils, and are similar to those of Hyophila involuta (Hook.) Jaeg. & Sauerb. Whitehouse (1976) has discussed the considerable variation in size and degree of ornamentation of propagula of B. arcuata.

Barbula arcuata is similar to B. indica in the red, spiculate, usually highly twisted peristome. The two species often grow intermixed. In hygric habitats, the leaves of B. indica are more flaccid than usual and may be confused with those of B. arcuata. Barbula arcuata differs from B. indica in the long-triangular leaves with 1-3 apical teeth, costa abaxially smooth or sharply crenulate by projecting cell cross walls, adaxial surface of costa often bulging, not in a groove, adaxial stereid band of costa often nearly as large as the dorsal, and laminal cells smooth, short-rectangular.



*BARBULA* subgenus *HYOPHILADELPHUS* (C. Müll.) Zander, stat. nov.

Basionym: *Barbula* sect. *Hyophiladelphus* C. Müll., Syn. Musc.  
1: 604. 1848. Type: *Barbula agraria* Hedw. (lectotype).

Synonyms: *Tortula* sect. *Hyophiladelphus* (C. Müll.) Broth., Nat.  
Pfl. 1(3): 429. 1902.

*Barbula* sect. *Agrariae* Steere in Grout, Moss Fl. No. Amer. 1(3):  
173. 1938, nom. illeg. Type species: *Barbula agraria*  
Hedw.

Steere (1938) speculated, with good reason, that *Barbula agraria* Hedw. was probably sufficiently different from both *Barbula* and *Tortula* to justify the designation of a new genus. I agree that it is rather distinctive but recognize it here in a monotypic subgenus. The salient character states of subg. *Hyophiladelphus* are the long, red, spiculose, twisted peristome teeth, the revoluble annulus, the moderately differentiated perichaetial leaves, the spatulate, epapillose leaves with adaxially strongly bulging cell walls, and the costa sharply mucronate, with two stereid bands and ventral surface of longitudinally elongate cells. *Luisierella barbula* (Schwaegr.) Steere has a similar strongly colliculate adaxial laminal surface and nearly smooth abaxial surface, but the peristome is not twisted, the leaves are ligulate, the laminal cells have rounded, not quadrate lumens, the costa has an adaxial epidermis of cells similar to those of the lamina, and propagula are often present.

11. *Barbula agraria* Hedw., Spec. Musc. 116. 1801. Type: "Jamaica et Domingo," Swartz s.n. (G—syntype, BM—syntype?).

Synonyms: *Tortula agraria* (Hedw.) P. Beauv., Prodr. 91. 1805.

*Bryum stellatum* Dicks. ex With., Syst. Arr. Brit. Pl. ed. 4, 3:  
796. 1801. Type: Anon., s.n. (BM—holotype?). — *Tortula stellata* (Dicks. ex With.) Sm., Fl. Brit. 3: 1254. 1804.  
— *Barbula stellata* (Dicks. ex With.) Brid., Mant. Musc.  
88. 1819.

*Tortula linearifolia* P. Beauv., Prodr. 92. 1805.

*Tortula pallens* Brid., Spec. Musc. 1: 246. 1806. — *Barbula pallens* (Brid.) Brid., Mant. Musc. 88. 1819.

*Tortula decipiens* Brid., Spec. Musc. 1: 247. 1806, nom. inval.  
incl. spec. prior. [*T. linearifolia* P. Beauv., 1805].

Barbula acuminata Brid. in Roehl., Deutsch. Fl. Krypt. ed. 2, 3: 79. 1813 non. B. acuminata Hedw., 1801. -- Barbula agraria var. acuminata (Brid.) Brid., Mant. Musc. 88. 1819. -- Tortula agraria var. acuminata (Brid.) Mont., Ann. Sci. Nat. Bot. ser. 2, 14: 347. 1840.

Barbula domestica Brid., Mant. Musc. 89. 1819. Type: Antilles, Richard s.n. (BM--isotype).

Barbula latifolia Brid., Bryol. Univ. 1: 536. 1826. -- Tortula latifolia (Brid.) Mont. in Ramon de la Sagra, Hist. Fis. Cuba Bot. Pl. Cell. 513. 1838-1842 non T. latifolia Bruch ex Hartm., 1832.

Barbula rauii Aust., Bull. Torrey Bot. Cl. 6: 43. 1875.

Barbula husnotii Schimp. ex Besch., Ann. Sci. Nat. Bot. ser. 6, 3: 199. 1876, syn. nov. Type: Martinique, Gueydon, and Guadeloupe, Basse-Terre and bridge of Noire R. (apparently a mixture), Husnot s.n. (Husnot, Pl. des Antilles 139) (BM, FH--isotypes). -- Tortula husnotii (Schimp. ex Besch.) Broth., Nat. Pfl. 1(3): 429. 1902.

Barbula subagraria C. Müll., Bull. Herb. Boiss. 5: 193. 1897. -- Tortula subagraria (C. Müll.) Broth., Nat. Pfl. 1(3): 429. 1902.

Barbula agraria fo. involuta Biz. & Thér., Mem. Soc. Cub. Nat. Hist. 13: 273. 1939, nom. inval. descr. gall., syn. nov. Type: Cuba, Oriente, Baracoa, Ekman 4490 (FH--isotype).

Barbula agraria was illustrated and described by Bartram (1949), Breene (1963), Crum and Steere (1957), and Steere (1938). Crum (1951) gave the distribution of this common tropical moss as U.S.A. (Florida, Louisiana, Texas), Mexico (Campeche, Hidalgo, Quintana Roo, San Luis Potosí, Veracruz, Yucatán), Guatemala, West Indies, and northern South America. The habitat includes soil, rocks, walls, coral, limestone, sandstone, brick, from near sea level to 350 m elevation. Although certain other species of Barbula (B. arcuata, B. indica) that are also widespread in tropical America have proven to be pantropical, B. agraria is apparently a New World endemic. There are no closely related species. Species of Hyophila also have an areolation of epipillose, adaxially bulging cells. But these species have laminal cells with evenly thickened walls, subquadrate to rounded lumens and a yellow-brown color cast, giving a far different appearance. The areolation of B. agraria is of thin-walled, rectangular cells and lumens, with a clear to light yellow coloration.

Although it has a spatulate leaf shape and long, twisted peristome of 32 spiculate teeth, B. agraria differs from Tortula species in the distinctive leaf areolation and the costa having two stereid bands. It differs from other species of Barbula in the areolation,

the revoluble annulus, and the spatulate leaf shape. A further difference may be in sexual condition. *Barbula* species are consistently dioicous. Most authors (including Hedwig, 1787-1797) who have described *B. agraria* (under synonyms) apparently have been unable to determine sexual condition. However, Swartz (1806) indicated that this species has distinct androgametophytes, but Miller (1949) described it as monoicous, the androecia being terminal on a basal branch. In fact, perigonia are very difficult to locate and are absent, seemingly, in many collections. When found, they occur on what appear to be separate, minute androgametophores that grow contiguous to the gynogametophores. The possibility that *B. agraria* is rhizautoicous, remains, is taxonomically important, and should be tested in experimental cultivation.

*PSEUDOCROSSIDIUM* Williams, Bull. Torrey Bot. Cl. 42: 396. 1915.

Type species: *Pseudocrossidium chilense* Williams.

Synonyms: *Barbula* sect. *Revolutae* B.S.G., Bryol. Eur. 2: 89.

1842 (fasc. 13-15 Mon. 27), syn. nov. Type species:

*Barbula revoluta* Brid. in Schrad. -- *Barbula* subsect.

*Revolutae* (B.S.G.) Chen, Hedwigia 80: 209. 1941.

As discussed by Zander and Steere (1978b), this genus is distinguished from *Barbula* mainly by the trend to elaboration of parts of the leaf as photosynthetic organs, either in differentiation of a pad of adaxial costal filaments, as is found in *Crossidium* Jur. of the Pottiaeae, or of thin-walled, hollow-papillose cells of the interior of the often spiral-revolute upper leaf margins, as in certain species of *Tortula* sect. *Cuneifoliae* (B.S.G.) Spruce, or both elaborations may occur in the same species. Character states associated with the strongly revolute margins are thickening of the superficial laminal cell walls, often of a deep yellow-brown color, of the exposed adaxial laminal surface near the margins. This thickening is only medial on the abaxial surface of the leaf. Additional characters are leaves usually lacking an adaxial stereid band, and perichaetial leaves usually highly differentiated, convolute-sheathing and largely prosenchymatous in most species. Although many specimens of *Pseudocrossidium* species are similar to *Tortula* in having only one stereid band, *Pseudocrossidium* is easily distinguished from *Tortula* by the differentiation of an abaxial costal epidermis. This consists of one layer of either comparatively thin-walled, wide-lumened cells or thick-walled cells with small, semi-circular lumens, or intergradations between these expressions. An abaxial costal epidermis is lacking or rarely poorly differentiated in *Tortula*. This convenient distinction has not been previously recognized and one might expect to find further synonyms in *Tortula* that rightly belong in *Pseudocrossidium* if other characters agree. *Pseudocrossidium* is, however, similar to *Tortula* in the presence of Begleiter (leaf strand) cells. These are located between the abaxial stereid band and the guide cells in *P. apiculatum*, *P. aureum*,

P. leucocalyx, P. replicatum and P. revolutum. I have never seen Begleiter cells in costal sections of species of Pleuroweisieae; however, these occur in some taxa of Barbuleae (e.g. Barbula unguiculata, B. orizabensis) and in many taxa of Pottieae, including species of Tortula and Crossidium. Pseudocrossidium is somewhat intermediate in character between Barbula sect. Barbula and Tortula, but is probably best placed in the Barbuleae near Barbula on the basis of the abaxial costal epidermis and the occasional presence of an adaxial stereid band in the costa of some species.

Pseudocrossidium species appear to form a north-south gradient in morphological elaboration, in that North American and European species lack some of the salient characters distinguishing the South American species (see appended key to South American species). The northernmost-ranging species, P. revolutum, is much reduced in size and lacks most of the distinguishing characters of the genus but is related through P. aureum and P. replicatum.

12. Pseudocrossidium revolutum (Brid. in Schrad.) Zander, comb. nov.

Basionym: Barbula revoluta Brid. in Schrad., Jour. Bot. (Gott.) 1800(2): 299. 1801.

Synonyms: Tortula revoluta (Brid.) Schrad., Bot. Zeit. Regensburg 1: 214. 1802.

Barbula platyneura C. Mill. & Kindb. in Macoun, Cat. Canad. Pl. 6: 52. 1892, syn. nov. Type: Canada, British Columbia, Deer Park, Arrow Lake, Macoun 244 (CANM--isotype).

Desmatodon ellesmerensis Brassard, Bryologist 74: 208. 1971, syn. nov. Type: Canada, Northwest Territories, Ellesmere Is., 82° 30'N, 62° 20'W, Brassard 4467 (BUF--isotype).

Pseudocrossidium revolutum is described and illustrated by European authors as Barbula revoluta, a synonym. This species is widespread in Europe, western Asia and northern Africa (Podpěra, 1954), and occurs in South Africa fide Index Muscorum (van der Wijk et al., 1959-1969). I have seen New World material (cited below) of P. revolutum from several areas in north Canada and from the Pacific Coast of Canada and the U.S.A. When present, the convolute-sheathing perichaetial leaves and the propagula borne on the adaxial surface of the costa easily distinguish P. revolutum from the very similar southern species P. replicatum. However, none of the North American specimens bore sporophytes and in only one (isotype of B. platyneura at DUKE) were propagula found on the leaves. However, the small plant size and weakly recurved leaf margins that are not or weakly differentiated as photosynthetic organs indicate appropriate referral to P. revolutum. The gametophores regenerating in experimental culture from U.S.A., California, Galloway 242 (H.L.K. Whitehouse, pers. comm.) formed differentiated perichaetial leaves quite unlike those of P. replicatum. An Ecuadorian specimen in a small

packet glued to a sheet together with the type of *Barbula replicata* Tayl. at BM is possibly *P. revolutum*. It has the highly differentiated perichaetial leaves seen in European collections of *P. revolutum* and the capsules are much smaller than those of *P. replicatum*, being only 1.1-1.3 mm long. The leaves are similar to those of *P. revolutum*, but this fragmentary specimen may be only a poorly developed form of *P. excavatum* (Mitt.) Williams, which normally has well-developed marginal photosynthetic organs (see key below).

North American specimens of *P. revolutum* have apiculate to short-mucronate, subacute to blunt leaf apices that are similar to *P. revolutum* in Europe, but are perhaps more strongly mucronate. The synonym *Barbula platyneura* was indicated by Steere (1938) to be an "American counterpart of the European *B. hornschiuchiana*." However, the latter is distinguished from *P. revolutum* by the very narrowly acute leaf apex with a strongly excurrent mucro, and apparently never produces propagula. A combination in *Pseudocrossidium* is given here for this European taxon.

*Pseudocrossidium hornschiuchianum* (Schultz) Zander, comb. nov.

Basionym: *Barbula hornschiuchiana* Schultz, Flora 5(Syll.): 36. 1822.

Synonyms: *Barbula revoluta* var. *hornschiuchiana* (Schultz) Brid., Bryol. Univ. 1: 572. 1826. -- *Tortula hornschiuchiana* (Schultz) De Not., Syll. 179. 1838. -- *Tortula revoluta* var. *hornschiuchiana* (Schultz) De Not., Mem. Roy. Acc. Sci. Torino 40: 315. 1838.

Combination of these European names in the heretofore exotic genus *Pseudocrossidium* may be disconcerting to some bryologists; however, it is possible that the study of neotropical taxa is the key to understanding the relationships of many European species.

New World collections of *P. revolutum*, other than the types cited above, include: Canada, Yukon, Firth River Basin, lower Manche Creek, Sharp 58219b (NY); U.S.A., Oregon, Sherman Co., along White R. tributary, Deschutes R., Pechanec 1259 (herb. G.R. Brassard), California, San Diego Co., Descanso Distr., Cleveland National Forest, Boulder Creek Rd., Galloway 242 (CSPU). Possibly *P. revolutum* is: Ecuador, Pichincha, Quite, Jameson s.n., as "*Tortula replicata*?" (BM). The habitat includes soil, rocks, north-facing cliffs, calcareous outcrops and soil, from 75-1050 m elevation.



13. Pseudocrossidium replicatum (Tayl.) Zander, comb. nov.

Basionym: Barbula replicata Tayl., London Jour. Bot. 5: 49. 1846. Type: Ecuador, Pichincha, Quito, walls, Jameson, 1847 (BM, NY--isotypes).

Synonyms: Tortula replicata (Tayl.) Wils., London Jour. Bot. 5: 454. 1846.

Barbula spiralis Schimp. ex C. Müll., Syn. Musc. 1: 622. 1849, syn. nov. Type: Mexico, Veracruz, Yareta, Mirador, Liebmann, 1842 (BM--isotype). — Tortula spiralis (Schimp. ex C. Müll.) Mitt., Jour. Linn. Soc. Bot. 12: 151. 1869.

Barbula apiculata Hampe, Linnaea 31: 519. 1862 non B. apiculata Hedw., 1801. — Tortula apiculata Mitt., Jour. Linn. Soc. Bot. 12: 153. 1869 (nom. nov. for B. apiculata Hampe) non T. apiculata (Hedw.) Turn., 1804.

Barbula perlinearis C. Müll., Bull. Herb. Boiss. 5: 195. 1897, syn. nov. Type: Guatemala, Quezaltenango, Bernoulli & Cario 118 (NY--isotype).

Barbula spiralis var. emarginata Card., Rev. Bryol. 36: 84. 1909, syn. nov. Type: Mexico, México, Amecameca, Pringle 10611 (BM, MEXU, F, FH--isotypes).

F. Bowers (pers. comm.) has studied Pseudocrossidium and agrees with me that P. replicatum is appropriately placed in this genus. This species is unusual but not alone in the genus in having only weakly differentiated perichaetial leaves and the costa being merely mucronate, not short-awned. However, the strongly spiralled leaf margins, with thin-walled, hollow-papillose, deeply chlorophyllose interior cells, the upper laminal cells papillose medially but becoming epapillose towards the margins (on the exposed lamina), and the distinctive transverse section of the costa that shows only one stereid band and often Begleiter cell development, are in combination diagnostic features. It is closely related to P. aureum, in which the margins are not modified as photosynthetic organs and the costa is short-awned. A specimen of P. replicatum from Ecuador (Tungurahua, Ambato, Spruce 231—NY) has a strongly excurrent costa similar to that of P. aureum. Both species may develop a characteristic line of large-lumened, superficially thick-walled cells, often of a deep yellow or orange color, abaxially at the juncture of the costa and lamina, though this is less common in P. replicatum than in P. aureum. There is also a close relationship of P. replicatum to P. revolutum, but P. replicatum has more strongly revolute leaf margins, never has the propagula that are commonly found at least in European collections of P. revolutum, and never develops convolute-sheathing, largely prosenchymatous perichaetial leaves.

14. Pseudocrossidium aureum (Bartr.) Zander, comb. nov.

Basionym: Tortula aurea Bartr., Bull. Torrey Bot. Cl. 51: 339. 1924. Type: U.S.A., Arizona, Pima Co., Santa Catalina Mts., Bear Canyon, Bartram 307 (Bartram, Mosses So. Arizona 98) (FH—holotype, CU—isotype).

Synonym: Barbula aurea (Bartr.) Zander in Zander & Steere, Bryologist 81: 466. 1978.

This species was described and illustrated by Bartram (1924) and Steere (1938). It has been known from U.S.A.: Arizona, New Mexico and Texas (Steere (1938) and Mexico: Chihuahua, Coahuila, Hidalgo, San Luis Potosí, Sonora and Zacatecas (Crum, 1951). An additional locality is Mexico: Puebla, 6 km NW of Zacatepec, Delgadillo 3603b (MEXU). Its habitat is very dry or desert areas, on ledges, soil, canyon walls or rock outcrops, at 800–2350 m elevation. Magill (1976) noted that in Big Bend National Park in southwestern Texas, U.S.A., it is both locally abundant and the most frequently encountered moss of desert or grassland communities; Bartram (1924) indicated that it is common on dry ledges in the region of the type locality. The sporophytes of this species are unknown. The leaf margins vary between collections from broadly once-revolute to narrowly recurved. It is placed in Pseudocrossidium on the basis of the lack of an adaxial stereid band and presence of an abaxial epidermis in the costa, in addition to having Begleiter cells and the general appearance of the genus. Although closely related to P. replicatum, it differs in lacking marginal photosynthetic organs and in having a short awn. Pseudocrossidium aureum often has a row of large-lumened, cubical to short-oblong superficial cells, slightly larger than the laminal cells, abaxially along the juncture of the upper costa and leaf lamina. These distinctive cells are often superficially thick-walled and deep yellow-brown or orange in coloration, with the appearance of a row of ocelli.

\* \* \* \*

The foregoing key to taxa of Barbula and Pseudocrossidium will suffice for all species of Pseudocrossidium in North and Central America. The species in South America may be distinguished by the very tentative key given below, which is based largely on specimens at NY. I have not seen material of P. elatum or P. pachygatrellum. However, F. Bowers (pers. comm.) has studied the former species and believes it to be a Pseudocrossidium.

## KEY TO SPECIES OF PSEUDOCROSSIDIUM IN SOUTH AMERICA

1. Adaxial epidermal cells of costa in one layer above guide cells, not forming filaments..... 2.
1. Adaxial epidermal cells of costa in 2 to several layers above guide cells, usually differentiated as separate filaments..... 3.
  2. Leaf margins recurved, upper medial laminal cells with spiculose papillae centered over the bulging lumens; Chile..... P. leucocalyx (Mont.) Ther.
  2. Leaf margins once revolute to spiral-revolute, upper medial laminal cells with low, bifid to multiplex papillae apparently scattered over the weakly convex lumens; throughout Andes..... P. replicatum (Tayl.) Zander
3. Leaf margins not differentiated as photosynthetic organs..... 4.
3. Leaf margins spiral-revolute, interior cells strongly chlorophyllose, thin-walled, hollow-papillose..... 5.
  4. Leaves apiculate, costa percurrent, perichaetial leaves weakly differentiated; Peru.....  
.....P. elatum (Williams) Delgadillo
  4. Leaves obtuse, costa ending below apex, perichaetial leaves strongly differentiated; Chile... P. chilense Williams
5. Leaves 0.5-0.7 mm long, apiculate; Ecuador.....  
.....P. excavatum (Mitt.) Williams
5. Leaves 1.2-1.8 mm long, mucronate to short-awned..... 6.
  6. Leaves mucronate; Bolivia... P. pachygastrellum (Herz.) Broth.
  6. Leaves short-awned; Peru, Chile.....  
..... P. apiculatum Williams

## EXCLUDED TAXA

In a treatment of the genus Tuerckheimia (Zander, 1978c), I indicated that T. linearis (Web. & Mohr) Britt. should be recognized as Barbula linearis Web. & Mohr, because of a supposed close relationship to B. indica. This was incorrect, being based upon a series of specimens at NY that included both T. linearis and West Indian expressions of B. indica with unusually long leaves and often rather massive laminal papillae. Material, including an isotype of T. lineare, that had been examined by Britton (1913) and Crum and Steere (1957) for their discussions of T. lineare has been located at NY, for which I thank W.R. Buck. On examination of these specimens

and of the holotype ("Fl. Ind. Or." leg. Swartz s.n.) from SPA, I find that T. linearis is probably best recognized as Oxystegus linearis (Web. & Mohr) Hilp. The illustrations by Crum and Steere (1957), which I had suggested were probably O. tenuirostris (Hook. & Tayl.) A.J.E. Sm., are actually quite representative of most material of O. linearis. Oxystegus linearis is distinguished from Barbula indica by the broad costa with two layers of guide cells (in most collections), the lamina inserted laterally on the costa, not adaxially and thus not forming an adaxial laminal groove, and the basal laminal cells sharply differentiated, inflated, comprising an oval, somewhat sheathing leaf base. It differs from O. tenuirostris by the 32 anastomosing, filiform, closely spiculate, red peristome teeth borne on a distinct basal membrane, the weakly sheathing leaf base and the two layers of guide cells usually found in the costa. The differences in peristome structure between O. linearis and O. tenuirostris may seem extreme; however, Grout (1938b) noted similar variation to occur between different collections of Trichostomum jamaicense (Mitt.) Jaeg. in the West Indies. Also, many collections of Trichostomum species have peristomes lacking basal membranes, and the usual distinctions between the genera Oxystegus and Trichostomum seem to me rather arbitrary or even baseless in respect to peristome characters. Clarification of relationships between genera of Trichostomoideae await more intensive study, however.

Other North American species of Barbula that are not listed here or in the lists of synonymy cited above, or which are not treated in my review of Didymodon for North America north of Mexico (Zander, 1978a), are synonyms of species of Didymodon and will be discussed in a forthcoming paper on Didymodon in Mexico. However, Barbula crassicuspis H. Robinson is a synonym of Morinia crassicuspis (H. Robinson) Zander (Zander, 1978b).

#### CORRECTIONS

In a treatment of Didymodon in North America north of Mexico (Zander, 1978a), I dealt with the Didymodon fallax group of species as Didymodon sect. Graciles (Milde) K. Saito. However, an earlier name, noted in the Supplement to the Index Muscorum (van der Wijk et al., 1959-1969), is available at the sectional level.

Didymodon section Fallaces (De Not.) Zander, comb. nov.

Basionym: Tortula sect. Fallaces De Not., Mem. Roy. Acc. Sci. Torino 40: 287. 1838. Type species: Barbula fallax Hedw.

Synonyms: Barbula sect. Fallaces (De Not.) Steere in Grout, Moss Fl. No. Amer. 1: 174. 1938.

Barbula sect. Graciles Milde, Bryol. Siles. 117. 1869.

Type species: Barbula rigidicaulis C. Muell. --

Didymodon sect. Graciles (Milde) K. Saito, Jour. Hattori Bot. Lab. 39: 504. 1975.

Barbula subsect. Fallaciformes Kindb., Eur. No. Amer. Bryin. 2: 246. 1897.

Additional synonyms are given by Saito (1975).

In the same paper, Didymodon reedii H. Robins. was inadvertently left out of the key. "See ll. D. reedii" should be inserted next to D. brachyphyllus (Sull. in Whipple) Zander on page 17.

#### SUMMARY

Taxa recognized in North America:

Barbula Hedw. subg. Barbula

sect. Barbula

- B. unguiculata Hedw.
- B. orizabensis C. Mill.
- B. calcarea Ther.
- B. inaequalifolia Tayl.

sect. Convolutae B.S.G.

- B. indica (Hook.) Spreng. [s. ampl.]
- B. amplexifolia (Mitt.) Jaeg.
- B. convoluta Hedw.
  - var. convoluta
  - var. gallinula Zander, var. nov.
- B. eustegia Card. & Ther. [columb.]

sect. Hydrogonium (C. Mull.) K. Saito

- B. ehrenbergii (Lor.) Fleisch. [columb.]
- B. arcuata Griff. [s. ampl. & columb.]

Barbula subg. Hyophiladelphus (C. Mull.) Zander, stat. nov.

- B. agraria Hedw.

Pseudocrossidium Williams

- P. revolutum (Brid. in Schrad.) Zander, comb. nov.
- P. replicatum (Tayl.) Zander, comb. nov.
- P. aureum (Bartr.) Zander, comb. nov.

Other nomenclatural novelty:

Pseudocrossidium hornschurchianum (Schultz) Zander, comb. nov.



New taxonomic synonyms in *Barbula* and *Pseudocrossidium*  
 (basonyms of species alphabetized by epithet):

- Barbula* sect. *Revolutae* B.S.G. = *Pseudocrossidium*
- Barbula* *abbonii* Ther. = *Didymodon* *tophaceus*
- Barbula* *agraria* fo. *involuta* Bix. & Ther. = *B. agraria*
- Barbula* *convoluta* var. *propagulifera* Glow. = *Gymnostomum* *aeruginosum*
- Barbula* *crispula* Hampe in Jaeg. = *B. arcuata*
- Barbula* *cruegeri* Sond. ex C. Müll. = *B. indica*
- Barbula* *ehrenbergii* var. *mexicana* Ther. = *B. ehrenbergii*
- Desmatodon* *ellesmerensis* Brassard = *P. revolutum*
- Barbula* *erosa* Hampe in C. Müll. = *B. indica*
- Barbula* *ferrinervis* C. Müll. = *B. arcuata*
- Barbula* *ferrinervis* var. *eggersiana* C. Müll. = *B. arcuata*
- Tortula* *gregaria* Mitt. = *B. indica*
- Barbula* *haringae* Crum = *B. amplexifolia*
- Barbula* *horrinervis* K. Saito = *B. indica*
- Barbula* *husnotii* Schimp. ex Besch. = *B. agraria*
- Barbula* *hypselostegia* Card. = *B. indica*
- Barbula* *linguaeifolia* Bartr. = *B. calcarea*
- Barbula* *macrogonia* Besch. = *B. arcuata*
- Barbula* *microglottis* C. Müll. = *B. indica*
- Barbula* *muenchii* Card. = *B. indica*
- Barbula* *perlinearis* C. Müll. = *P. replicatum*
- Barbula* *platyneura* C. Müll. & Kindb. = *P. revolutum*
- Barbula* *pringlei* Card. = *B. indica*
- Barbula* *purpuripes* C. Müll. = *B. indica*
- Barbula* *rubricaulis* Ther. = *B. arcuata*
- Barbula* *rufipes* Schimp. ex Besch. = *B. indica*
- Trichostomum* *setifolium* C. Müll. = *B. arcuata*
- Barbula* *spiralis* Schimp. ex C. Müll. = *P. replicatum*
- Barbula* *spiralis* var. *emarginata* Card. = *P. replicatum*
- Barbula* *stenotheca* Ther. = *B. orizabensis*
- Barbula* *stillicidiorum* Card. = *B. arcuata*
- Barbula* *suberythropoda* C. Müll. = *B. arcuata*
- Barbula* *subulifolia* Sull. = *B. arcuata*
- Barbula* *unguiculata* fo. *propagulosa* Crum = *B. indica*
- Barbula* *whitehouseae* Crum = *B. eustegia*
- Barbula* *wrightii* Sauerb. in Jaeg. = *B. indica*

#### ACKNOWLEDGEMENTS

For valuable discussions, suggestions and criticism, and for bringing certain specimens to my attention, I thank L.E. Anderson, G.R. Brassard, W.R. Buck, H.A. Crum, F. Bowers, M.O. Hill, D. Horton, B.M. Murray, C. Delgadillo M., A.J. Sharp, W.C. Steere, D.H. Vitt and H.L.K. Whitehouse, among others. I am grateful to the curators of the herbaria mentioned in the text for loan of specimens. Especial thanks are given to P.M. Eckel for rendering the diagnosis into Latin and for doing the illustrations.

## LITERATURE CITED

- Argent, G.C.G. 1973. A taxonomic study of African Pterobryaceae and Meteoriaceae I. Pterobryaceae. Jour. Bryol. 7: 353-378.
- Bartram, E.B. 1924. Studies in Tortula as represented in southern Arizona. Bull. Torrey Bot. Cl. 51: 335-340.
- \_\_\_\_\_. 1926. Notes on the genus Husnotiella Cardot. Bryologist 29: 44-46.
- \_\_\_\_\_. 1949. Mosses of Guatemala. Fieldiana: Bot. 25: 1-442.
- Berthier, J. 1978. Analyse des capacites morphogenes du filament des Eubryales, pp. 223-241, in C. Suire (ed.), Congres International de Bryologie. J. Cramer, Vaduz, Germany.
- Best, G.N. 1905. A lesson in systematic bryology. Bryologist 8: 17-22, pl. II.
- Breen, R.S. 1963. Mosses of Florida, an Illustrated Manual. Univ. Florida Press, Gainesville, Florida.
- Britton, E.G. 1913. West Indian Mosses. I. Bull. Torrey Bot. Cl. 40: 653-676.
- Cardot, J. 1899. Etudes sur la flore bryologique de l'Amerique du Nord. Revision des types d'Hedwig et de Schwaegrichen. Bull. Herb. Boiss. 7: 300-380, pl. VII-X.
- Carlquist, S. 1966. The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. Brittonia 18: 310-335.
- \_\_\_\_\_. 1974. Island Biology. Columbia Univ. Press, New York.
- Crum, H.A. 1951. The Appalachian-Ozarkian element in the moss flora of Mexico with a check-list of all known Mexican mosses. Univ. Michigan, Ann Arbor, Michigan. Available from: University Microfilms, Ann Arbor, Michigan; Publication no. 3486. 504 pp. Dissertation.
- \_\_\_\_\_. 1956. Two new species of Barbula (Musci) from the Southwest. Southw. Nat. 1: 35-38.
- \_\_\_\_\_. 1965. Barbula eustegia, a moss new to Canada. Canad. Field-Nat. 79: 157.
- \_\_\_\_\_. & E.B. Bartram. 1958. A survey of the moss flora of Jamaica. Inst. Jamaica Bull., Sci. Ser. 8: 1-90.
- \_\_\_\_\_. & W.C. Steere. 1957. The mosses of Porto Rico and the Virgin Islands. New York Acad. Sci., Sci. Surv. Porto Rico Virgin Islands 7(4): 395-599.
- \_\_\_\_\_. & L.E. Anderson. 1973. A new list of mosses of North America north of Mexico. Bryologist 76: 85-130.
- During, H.J. 1977. A taxonomical revision of the Garovaglioidae (Pterobryaceae, Musci). J. Cramer, Vaduz, Germany.
- Flowers, S. 1973. Mosses: Utah and the West. Brigham Young Univ. Press, Provo, Utah.
- Gangulee, H.C. 1972. Mosses of Eastern India and Adjacent Regions, A Monograph. Fascicle 3 (Syrrhopodontales, Pottiaceae & Dicranales). H.C. Gangulee, Calcutta.
- Grout, A.J. 1938a. The species concept. Bryologist 41: 49-50.
- \_\_\_\_\_. 1938b. Moss Flora of North America North of Mexico. 1(3): 187-192, pl. 69-90. A.J. Grout, Newfane, Vermont.

- Hedwig, J. 1787-1797. Descriptio et adumbratio microscopico-analytica muscorum frondosorum nec non aliorum vegetantium e classe cryptogamica Linnaei novorum dubiisque vexatorum. Leipzig.
- Hilpert, F. 1933. Studien zur Systematik der Trichostomaceen. Bot. Centralbl. Beih. 50(2): 585-706.
- Kindberg, N.C. 1888-1891. Enumeratio Bryinearum Exoticarum Quam Alphabetice Disposuit. Linköping.
- Koch, L.F. & H.A. Crum. 1950. Mosses of Baja California. Rev. Bryol. Lichénol. 19: 188-192.
- Lawton, E. 1971. Moss Flora of the Pacific Northwest. Hattori Botanical Laboratory, Nichinan, Japan.
- Loeske, L. 1910. Studien zur Vergleichenden Morphologie und Phylogenetischen Systematik der Laubmoose. Max Lande, Berlin.
- Magill, R.E. 1976. Mosses of Big Bend National Park, Texas. Bryologist 79: 269-295.
- Manuel, M.G. 1974. A revised classification of the Leucodontaceae and a revision of the subfamily Alsiioideae. Bryologist 77: 531-550.
- Mayr, E. 1942. Systematics and the Origin of Species. Columbia Univ. Press, New York.
- Moenkemeyer, W. 1927. Die Laubmoose Europas, vol. 4 in L. Rabenhorst, Kryptogamenflora von Deutschland, Österreich und der Schweiz. Leipzig.
- Müller, C. 1849. Synopsis Muscorum Frondosorum. Vol. I. Berlin.
- Pianka, E.R. 1970. On r- and K-selection. Amer. Natur. 104: 592-597.
- Podpera, J. 1954. Conspectus Muscorum Europaeorum. Ceskosl. Akad. Ved, Prague.
- Pursell, R.A. 1973. Un censo de los musgos de Venezuela. Bryologist 76: 473-500.
- Saito, K. 1971. Notes on four species of the genus Barbula. Jour. Jap. Bot. 46: 55-59.
- \_\_\_\_\_. 1975. A monograph of Japanese Pottiaceae (Musci). Jour. Hattori Bot. Lab. 39: 373-537.
- Steere, W.C. 1938. Barbula, pp. 173-185 in A.J. Grout, Moss Flora of North America North of Mexico, 1(3). A.J. Grout, Newfane.
- \_\_\_\_\_. 1948. Contribution to the bryogeography of Ecuador. I. A review of the species of musci previously reported. Bryologist 51: 65-167.
- \_\_\_\_\_. 1978. The Mosses of Arctic Alaska. J. Cramer, Vaduz, Germany.
- Steere, W.C. & H.A. Crum. 1977. New combinations and new taxa of mosses proposed by Nils Conrad Kindberg. Mem. New York Bot. Gard. 28(2): 1-220.
- Swartz, O. 1806. Flora Indiae Occidentalis aucta atque illustrata sive descriptiones plantarum in prodromo recensitarum. Erlangen.
- Theriot, I. 1931. Mexican mosses collected by Brother Arsène Brouard III. Scithson. Misc. Coll. 85(4): 1-55.

- \_\_\_\_\_. 1939-1941. Complement au catalogue des mousses de Cuba et revision de plusieurs genres I-IV. Mem. Soc. Cub. Hist. Nat. 13: 202-222, 265-282, 14: 349-372, 15: 211-236.
- \_\_\_\_\_. 1944. Musci hispaniolenses. Rev. Bryol. 14: 7-25.
- Van der Pijl, L. 1972. Principles of Dispersal in Higher Plants. 2nd Ed. Springer-Verlag, New York.
- Van der Wijk, R., W.D. Margadant & P.A. Florschütz. 1959-1969. Index Muscorum. Reg. Veg. 17, 26, 33, 48, 65. Utrecht.
- Weber, W.A. & L.D. Simone. 1977. Tetraphis pellucida and T. geniculata: scindulae as diagnostic features in bryophytes. Bryologist 80: 166-167.
- Welch, W.H. 1950. A contribution to the bryophyte flora of Cuba. Bryologist 53: 238-243.
- Whitchouse, H.L.K. 1966. The occurrence of tubers in European mosses. Trans. Brit. Bryol. Soc. 5: 103-116.
- \_\_\_\_\_. 1973. The occurrence of tubers in Pohlia pulchella (Hedw.) Lindb. and Pohlia lutescens (Limpr.) Lindb. fil. Jour. Bryol. 7: 533-540.
- \_\_\_\_\_. 1976. Does Ceratodon purpureus (Hedw.) Brid. have tubers? Jour. Bryol. 9: 177-184.
- Wilczek, R. & F. Demaret. 1976. Trois Barbula propagulifères de Belgique. Dumortiera 5: 1-3.
- Zander, R.H. 1968. Barbula inaequalifolia Tayl. new to North America. Bryologist 71: 41-44.
- \_\_\_\_\_. 1976. Notes on Pottiaceae in Middle America. Bryologist 79: 227-231.
- \_\_\_\_\_. 1977. The tribe Pleuroweisieae (Pottiaceae, Musci) in Middle America. Bryologist 80: 233-269.
- \_\_\_\_\_. 1978a. New combinations in Didymodon (Musci) and a key to the taxa in North America north of Mexico. Phytologia 41: 11-32.
- \_\_\_\_\_. 1978b. A synopsis of Bryoerythrophyllum and Morinia (Pottiaceae) in the New World. Bryologist 81: 539-560.
- \_\_\_\_\_. 1978c. Synopsis of the genus Tuerckheimia (Pottiaceae). Misc. Bryol. Lichenol. 8(2): 25-28.
- \_\_\_\_\_. & W.C. Steere. 1978. Tortula scotteri sp. nov. from the Northwest Territories of Canada. Bryologist 81: 463-467.